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A Comparison of Coyote Diets in Urban and Rural Habitats in the Piedmont of South Carolina

Bethany Krug

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To the Dean of the Graduate School:

We are submitting a thesis written by Bethany Krug entitled “A COMPARISION OF COYOTE DIETS IN URBAN AND RURAL HABITATS IN THE PIEDMONT OF SOUTH CAROLINA.”

We recommend acceptance in partial fulfillment of the requirements for the degree of Master of Science in Biology.

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A COMPARISION OF COYOTE DIETS IN URBAN AND RURAL HABITATS IN THE PIEDMONT OF SOUTH CAROLINA

A Thesis

Presented to the Faculty

Of the

College of Arts and Sciences

In Partial Fulfillment

Of the

Requirements for the Degree

Of

Master of Science

In Biology

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April 2020

By

Bethany Krug

Abstract

With increasing rates of urban expansion, interactions between humans and wildlife become inevitable. These urban environments present novel situations to native species, frequently resulting in their displacement or extirpation. However, some species, often referred to as “urban adapters”, have thrived in these landscapes. Coyotes (*Canis latrans*) are a prime example of a species that has adapted to exploit urban habitats. Coyotes are omnivores with food choices ranging from small/medium mammals to invertebrates depending on habitat. With their recent range expansion into the Southeast, little is known of their behavioral ecology in the region, especially details relating to their diet. Macroscopic and stable isotope analyses of scat were used to study the diets of rural and urban coyotes in the Piedmont Region of South Carolina to assess the relative content of anthropogenic food sources in their diet. Over three time intervals (breeding, 1 January- 30 April; pup-rearing, 1 May-31 August; dispersal, 1 September- 31 December), 20 scats were collected from 13 sites; 10 scats were urban, and 10 scats were from rural locations. Macroscopic materials were separated into categories of bone, hair, seeds, vegetation, insect exoskeletons, and anthropogenic materials. To identify the presence of anthropogenic food sources that may not have been visible macroscopically, stable isotope analysis was used. Higher $\delta^{13}C$ content is an indication of potential anthropogenic food sources due to corn-based foods being a primary staple of human diet in the region. I hypothesized that urban coyote diets would contain more anthropogenic food sources and thus have higher carbon levels compared to rural diets. I found that there was no significant difference in ^{13}C and ^{15}N isotope levels in coyote

scats between rural and urban environments overall. Nor was there a significant difference in ^{13}C and ^{15}N isotope levels between rural and urban habitats across seasons. Furthermore, I found no difference between macroscopic components between rural and urban coyote scats.

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Introduction

Global change

The expansion of the human population across the globe has dramatically altered landscapes. As a result, native habitats have been placed under novel and extreme pressures, changing the dynamics of ecosystems. Perhaps one of the most significant effects humans have had on the environment is climate change. Global average temperatures have increased by ~1.8 ̊C over the last 115 years (1901-2016) (Wuebbles et al. 2017). However, climate change is not simply a rise in mean temperatures; there are further comprehensive effects on other systems, such as oceans. For example, global sea levels have risen 18 to 20 centimeters since 1900, with almost half of the increase (~40%) occurring since 1993 (Wuebbles et al. 2017). Moreover, in addition to climate change, humans have destroyed terrestrial habitats through processes such as deforestation. Hansen (2013) found that between 2000 and 2012, 2.3 million square kilometers of global forest has been lost.

The primary factor contributing to these effects is overpopulation. As of May 2019, the human population was 7.7 billion, a massive increase after only reaching 1 billion in 1800 (Roser et al. 2020). Exponential human population growth has led to the unsustainable development of infrastructure to accommodate these numbers, therefore expanding urban centers and reducing natural areas (Roser et al. 2020; Gehrt 2010). While there is a lack of agreement concerning the definition of “urban”, Gehrt (2010) cites the various definitions used in ecology and consolidates them into a general definition of areas where large groups of people and buildings aggregate and comprise a town or city. The structure of urban centers and the surrounding areas is designed for the benefit of one species, humans. The urban environment is built for our needs, resulting in homogenization of the landscape and this uniformity of urban areas in turn promotes biological homogenization of ecosystems (McKinney 2006).

However, across the world, there are species called “urban adapters” that now successfully inhabit these anthropogenic habitats. Species that thrive in urban habitats are typically invasive or immigrant organisms that take advantage of a niche not being occupied as few species can tolerate highly urban environments (McKinney 2006). While some urban adapters have been able to flourish in these altered landscapes, the overall effect on native flora and fauna has been deleterious. A global review reported that with increasing urbanization there is a decline in native species abundance and a decrease in biotic interactions overall as well as reduced ecosystem complexity (McKinney 2006). In contrast, the same review reported that with increasing urbanization there is an increase in both biomass of urban adapters and total population abundance of such species (McKinney 2006). Urban adapted organisms are often supported based on the availability of resources such as trash and the small prey species that use that refuse (Bateman and Fleming 2012). Furthermore, urban adapted animal species use buildings for cover and can be deliberately fed by people (Bateman and Fleming 2012).

Terrestrial landscapes are not the only habitats affected by urbanization. This urbanization of natural landscapes has significant effects on stream structure, which in turn effects stream ecosystems. Violin et al. (2011) found that urban degradation leads to stream ecosystems that are biologically distinct from naturally occurring streams and cannot be successfully mitigated by restoration. Ephemeroptera, Plecoptera, and Tricoptera (EPT) are aquatic invertebrate taxa that provide information about stream water quality and are commonly used to assess the effects of pollution (Reif 2002). Violin et al. (2011) found that the macroinvertebrates inhabiting such streams were typically those identified as more tolerant species and were usually non-EPT taxa, showing that pollution was probably affecting these streams.

Urbanization often affects native plants due to the increase of impervious surfaces and installations of non-native ornamental species (McKinney 2008). Plant species richness may increase at intermediate levels of urbanization, but this effect is primarily due to introduced plants outpacing extinctions of native species (McKinney 2008). This decrease in native plants can in turn decrease some of the vertebrate species present in urban habitats (McKinney 2008).

Vertebrate groups are also affected by urbanization. Numerous species of amphibians have been noted to experience drastic reduction in numbers and local extirpations due to urban sprawl destroying their wetland habitats (Scheffers and Poszkowski 2012).While various species of birds inhabit urban and suburban environments, a review of reproductive success found that birds are also negatively affected by urbanization (Chamberlain et al. 2009). Those researchers found that the species they observed in urban habitats had earlier laying dates, lower clutch sizes, lower nestling weights, and lower productivity per nesting attempt (Chamberlain et al. 2009).

Several studies around the world have detected a decrease of overall mammal species abundance in urban areas (Gomes et al. 2011; Lopucki and Kitowski 2017). Mammals have undergone noticeable effects of urbanization with many medium and large-sized species being completely extirpated from their native habitats, often as a result of human persecution. On the other hand, smaller mammals, including those associated with humans such as the house mouse (*Mus musculus*), tend to persist more in urban than in rural ecosystems (Gomes et al. 2011). The presence of these small mammals provides prey options for urban predators such as raptors and a few mammals. Although there are some conflicting results concerning mammal species' occurrence in urban habitats, the majority of research demonstrates mammal diversity overall is reduced in urban environments because the lack of natural habitat and connectivity to city outskirts confines species and inhibits dispersal both in and out (Lopucki and Kitowski 2017).

However, some mammals seem to be able to adapt to urban environments better than others. For example, raccoons (*Procyon lotor*) have thrived alongside humans. In Chicago, IL, researchers found that raccoon densities are higher in urban and suburban areas than in rural areas (Randa and Yunger 2006). This high density is likely due to a stable supply of anthropogenic food sources (Randa and Yunger 2006). Red foxes (*Vulpes vulpes*) have also been shown to thrive in urban environments. As omnivorous organisms, they are able to make use of a variety of food resources. In Estonia, they were reported in 70% of surveyed urban areas and were frequently sighted in city centers (Plumer et al. 2014). Those researchers reported that the foxes not only visited urban centers for food but even built pupping dens in heavy traffic areas (Plumer et al. 2014). Similar to raccoons and red foxes, coyotes (*Canis latrans*) commonly inhabit urbanized areas. Coyotes are found in many major cities all over the United States including large metropolitan areas like Chicago, IL and Denver, CO (Morey et al. 2007; Poessel et al. 2017a). A large quantity of research has been done in these cities due to organizations such as the Urban Coyote Project in Chicago conducting long term studies. In southern California, coyote probability of occurrence increases with both proximity and intensity of urbanization (Ordeñana et al. 2010).

Natural History of Coyotes

Distribution

The coyote's current distribution stretches across the entire United States and most of Canada and extends as far down as Panama in Central America (Hody and Kays 2018). Recent research has mapped the distribution of coyotes from before Europeans settled in North America. Prior to European settlement, coyotes were found in the western United States from California to as far east as Texas and Indiana (Hody and Kays 2018). Those researchers provided three factors that could have contributed to the coyote's rapid expansion in North America since 1900. First, the extinction of apex predators lowered coyotes' predation risk and created more niches for coyotes to expand into (Hody and Kays 2018). These apex predators included wolves (*Canis lupus*) and cougars

(*Puma concolor*) which typically don’t thrive in urban areas as well as coyotes do. Second, the conversion of forested landscapes to agricultural landscapes could have created a more suitable habitat for coyotes (Hody and Kays 2018). Finally, hybridization of coyotes with wolves and domestic dogs in Eastern North America introduced new genetic material that could promote survival (Hody and Kays 2018).

Thornton and Murray (2014) found that a large niche shift in hybrid expansion zones can lead to niche divergence in coyote populations that have recently expanded to the east coast of the United States. In addition, their work showed that coyote/wolf hybridization and other genetic variations can allow for greater changes in niche space which can lead to increased invasiveness (Thornton and Murray 2014). In the United States, coyotes used two expansion routes when they shifted from the west, one in the north and the other in the south. Their expansion into the northeast was rapid due to higher levels of hybridization with wolves resulting in new genotypes that could have favored colonization and survival (Hody and Kays 2018). The expansion of coyotes into the southeastern US occurred more slowly, and coyotes only began expanding in the 1960’s up until the 2000’s in some regions (Hody and Kays 2018).

Coyotes entered the Carolinas around the 1980s and 1990s (Hody and Kays 2018). Bozarth et al. (2011) found low haplotype diversity in South Carolina coyotes which was attributed to the founder effect as the population had only been established recently and by a small number of individuals compared with populations in the surrounding states.

Life History

Coyotes are one of the eight recognized species in the genus *Canis,* three of which are in the United States (Bekoff and Gese 2003). They have the ability to occupy numerous habitats all over the continental United States and many parts of Canada. These natural habitats include grasslands, deserts, mountains, and forests. Coyotes are identified by the blend of their gray and red pelage. They are typically smaller than gray wolves (*Canis lupus*). They can reach 1 to 1.5 meters in length depending on geographic location; coyotes in the northeastern United States tend to be larger than in the west (Bekoff and Gese 2003; Thornton and Murray 2014). They have an average lifespan of 13.5 to 15.5 years and occur in packs of anywhere from four to seven or more individuals, depending on food availability (Bekoff and Gese 2003).

Natural Diet of Coyotes

Coyotes choose habitats based on resource availability, especially food and water sources (Bekoff and Gese 2003). They are opportunistic omnivores who consume a variety of foods including fruits, invertebrates, birds, rodents, lagomorphs and even large ungulates such as elk (*Cervus canadensis*) and moose (*Alces alces*) (Bekoff and Gese 2003).

Coyote dietary needs can be influenced by the presence of pups. A litter can be up to six pups who don't emerge from the den until around three weeks of age and reach adulthood around nine months (Bekoff and Gese 2003). When provisioning young after weaning, parents are required to consume more energetically "profitable" foods to sustain their pups (Bekoff and Gese 2003).

Coyote dietary needs are also under seasonal influence (Bekoff and Gese 2003). A study of urban coyotes conducted in Denver, Colorado, found that fruit was the most common component of coyote diet during summer (Poessel et al. 2017a). In addition, the authors found deer hair in summer, which they concluded was present due to predation on fawns during the time of scat collection; lagomorphs and rodents were the most common prey in winter (Poessel et al. 2017a). In Chicago, Illinois, a study of the diet of urban coyotes found that rodents were most common during breeding and pup-rearing seasons (Morey et al. 2007). In contrast to the Denver study's findings, the Chicago researchers reported that deer were present throughout all seasons, possibly due to the availability of road-killed carrion (Morey et al. 2007).

Human-Coyote Conflict

While most species struggle to survive under the threat of habitat destruction, coyotes have thrived in altered landscapes, though not without resistance. Coyotes are often the largest carnivores in an urban habitat and their presence can cause concern for the public (Alexander and Quinn 2012). This anxiety stems from lack of understanding of coyote behavior and the negative reputation that they possess. However, with this successful adaptation to anthropogenic areas comes the potential for conflict. Poessel et al. (2017b) defined human-coyote conflict as a coyote attacking a human or pet as well as a coyote displaying aggressive behaviors such as growling, baring teeth, stalking, or other behaviors that could threaten a human. A comprehensive study surveyed 105 urban areas across the United States to understand the environmental factors that influence the occurrence of coyotes and conflict with humans in urban areas (Poessel et al. 2017b). The authors found that 80% or more of the large and medium urban areas studied reported instances of conflict (Poessel et al 2017b). Such occurrences have also been documented in U.S. locations such as Denver, Los Angeles, and in Calgary, Canada (Lukasik and Alexander 2008; Poessel et al. 2017a; Baker 2007). In Canada, Lukasik and Alexander (2008) saw a trend of greater amounts of pet fur in scats in areas with increased reports of conflict. They attributed the increased levels of refuse in scats to an elementary school being present in the region, something that could further increase the chances for conflict. Trash from the students was present on the school playground (Lukasik and Alexander 2008). In Denver, researchers found that conflicts were often higher in winter, suggesting that coyotes may take more risks in times of lower resource availability, such as moving into an area with a higher human presence (Poessel et al. 2017b).

Reports of conflict are often exaggerated, especially in the media, which in turn alters the public's perception of coyotes. In an analysis of their representation in Canadian media, Alexander and Quinn (2012) found that coyotes were negatively presented with 185 articles mentioning coyotes "attacking" when there were only 32 identified "attacks" in a 12-year period. Reports often included terms that elicited an emotional response including "nuisance", "wiley", "mangy" and "brazen" (Alexander and Quinn 2012). In addition, common concerns from the public were related to the safety of children and pets as well as the chance of disease transmission (Alexander and Quinn

2012). Such negative perceptions can influence management practices and make co-existence between humans and wildlife difficult.

Coyotes that have habituated to humans alter their behaviors. They will use roads as corridors and research shows they use them more frequently at night, perhaps because there are fewer cars on the road (Poessel et al. 2016). Vehicle collisions are often the most common cause of mortality for urban coyotes (Gehrt 2007). Coyotes were also found to be more likely to move into urban areas during the night when their likelihood of encountering a human would decrease (Poessel et al. 2016). Rural coyotes are also not safe from human persecution, due to their threat to livestock, with trapping and hunting being a significant cause on mortality (Gehrt 2007).

Urban Coyote Life History

Coyote Spatial Ecology in Urban Habitats

The resource needs of coyotes can vary depending on geography. Current research reports conflicting accounts, likely due to regional differences in urbanization levels in our understanding of space use of urban versus rural areas. Most coyotes in urban areas occur as single individuals or in small packs that are either transient or have established large home ranges and smaller defined territories within. Those packs or individuals that establish a home range in urbanized landscapes often need larger territories to compensate for few available natural resources (Poessel et al. 2016). The Denver study found that coyotes made use of most land types that fell within their home range: rural, altered, and developed land (Poessel et al. 2016). Researchers in Chicago, using radio collars, found that coyotes were more likely to have a home range in areas with less development and they commonly avoided the highly urbanized habitats (Gese et al. 2012). For those coyotes that do reside in urban areas, the presence of tree cover and riparian areas were noted to be significant aspects of their home ranges (Dodge and Kashian 2013; Gese et al. 2012). Tree cover is likely important for coyotes to remain hidden from humans in addition to the presence of prey along forest edges (Dodge and Kashian 2013). Riparian areas also provide cover and a source of vegetation and water (Gese et al. 2012).

Urban territory use can vary between the sexes of coyotes. Compared with males, urban females often hold a bigger territory due to the need for den sites (Poessel et al 2016). Female coyotes have even been observed denning in storm water drains suggesting that coyotes will use urban structures (Poessel et al. 2016). Both sexes are opportunistic in habitat selection, making use of frequently altered landscapes. A study in Detroit, Michcigan, reported evidence of coyotes taking advantage of urban areas that had reverted to more natural habitats due to economic decline in the region (Dodge and Kashian 2013).

Coyote Diet in Urban Ecosystems

One of the greatest factors influencing the presence of coyotes is food availability. Coyotes are opportunistic feeders and use a wide range of the resources available in their home ranges. While there are other influences, the presence of anthropogenic food has been hypothesized as an important element relating to coyote settlement in urban ecosystems. In southern California, coyotes in the most urbanized areas had a significant abundance of foods associated with human activity in their diet (Fedriani et al. 2001). Those researchers also observed coyotes foraging in a landfill which supports the idea of coyote exploitation of human-related food sources.

In contrast to Gese et al. (2012), the California researchers concluded that the presence of anthropogenic foods resulted in higher coyote densities in urban areas than in the surrounding rural areas (Gese et al. 2012; Fedriani et al. 2001). There are also studies that show no difference in anthropogenic food sources being exploited between rural and urban habitats (Santana and Armstrong 2017). Reasons for the lack of difference could be the illegal disposal of garbage in rural areas increasing the availability of anthropogenic food sources there. However, Santana and Armstrong (2017) found that rural areas had a greater diversity of food sources. Similarly, researchers in Arizona found that 35% of the scats they analyzed contained evidence of food from anthropogenic sources including dog food and bread (McClure et al. 1995), which is significantly higher than what is reported from the majority of current research. Poessel et al. (2017a) found that coyote scats they collected were composed of only a small amount of anthropogenic food (<1%), but there were still anthropogenic foods present in 27 of 64 (42%) samples in both low- and high-density urbanization sites.

Because the movement of coyotes into the eastern part of the United States was relatively recent, the research on them in that region is limited. Grigione et al. (2011) found that diet diversity was greater in a protected wildland than a suburban habitat in Florida and that anthropogenic waste (trash, rope, and plastic wrappers) was found twice as often in scats from the suburban habitat.

Furthermore, the presence of anthropogenic waste varied seasonally, with 25% found in coyote scats from the dry season and 14% found in coyote scats from the wet season (Grigione et al. 2011). Such seasonal differences could have arisen from the availability of natural foods decreasing in the dry season resulting in coyotes searching for alternative food sources. Researchers in Chicago found similar results with anthropogenic food being most common in more developed sites and varying seasonally, with peaks during the pup-rearing and dispersal seasons (Morey et al. 2007). Those peaks were likely due to an increase in human activity during those time frames, resulting in high levels of refuse available (Morey et al. 2007).

Although anthropogenic food can make up a substantial portion of a coyote's diet, such foods could also be harmful. Murray et al. (2015) looked at how consuming human-related food sources affected coyote health and found that urban coyotes diets had less protein and were more likely to be diseased than those in rural habitats. That study utilized stable isotope analysis, which has only recently been being employed to look at dietary composition in hair and scats.

Stable Isotope Analysis

Using stable isotopes can clarify gaps in scat analysis by identifying more precisely the likely origin of the scat contents. Stable isotope analysis relies on natural variation in the abundance of carbon (C) and nitrogen (N) isotopes in organisms and typically uses the difference in the natural abundance of isotopes in different trophic levels in food webs to identify components of an organism's diet (Hutchinson 2002). Using isotope forms such as δ ^{13}C, δ ^{15}N, δ ^{18}O, δ^{2}H, and δ^{34}S, the movements of nutrients, molecules, particles and organisms can be traced across landscapes and between components of the biosphere (West et al. 2006). In turn, the isotopes can be used to reconstruct aspects of diet, ecology and environmental histories (West et al. 2006).

Quantities of carbon and nitrogen vary across trophic levels and can provide information about what organisms are consuming. The isotope ^{13}C is often used to assess the presence of anthropogenic food sources because of its prevalence in corn as feed for livestock and in processed human foods (Jahren and Kraft 2008). The higher the amount of anthropogenic food consumed, the higher the δ ^{13}C levels. Furthermore, C_4 plants such as corn have higher δ ^{13}C levels than do C_3 plants due to differences in photosynthesis (O'Leary 1988). The C_4 photosynthetic pathway is more efficient in fixing carbon than the C_3 pathway, resulting in relative enrichment δ ^{13}C level (O'Leary 1988). In a similar fashion, δ^{15}N values can provide information about protein content in an organism's diet as nitrogen is more enriched at higher tropic levels (DeNiro and Epstein 1981).

Stable isotope analysis has been used to evaluate anthropogenic foods in kit fox diets in the San Joaquin Valley, CA (Newsome et al. 2010). Employing this method, they found that kit fox scats and hair had higher ^{13}C and lower ^{15}N levels suggesting they exploit anthropogenic food sources (Newsome et al. 2010). By comparing the kit fox diet to that of the local human population, these researchers were able to conclude that, due to their isotopic levels being the same, that kit foxes were consuming anthropogenic materials (Newsome et al. 2010).

Present Study

There has been no research regarding the ecology of coyotes in the Carolina Piedmont region of South Carolina. However, at the Savannah River Site in southwestern South Carolina, Schrecengost et al. (2008) studied and provided the first account of coyote diets but only on individuals from rural habitats, which will be discussed later.

The present study assesses the diets of both rural and urban coyotes in the Carolina Piedmont region through macroscopic and stable isotope analysis of scats and compared the degree to which urban and rural coyotes exploit anthropogenic food sources. It is likely that coyotes inhabiting urban areas use dietary resources that are both intentionally and unintentionally made available through the presence of humans. Therefore, I hypothesized that $\delta\,^{13}C$ levels, as well as other evidence of anthropogenic foods, will be higher in scats collected from urban, compared to rural, sites. Furthermore, I predicted that anthropogenic food content would be higher in urban compared with rural coyote scats during dispersal season as natural food sources become scarcer at that time.

Materials and Methods

Study Sites

Coyote scats were collected between February 2019 and November 2019. Thirteen research sites were surveyed in York, Chester and Lancaster counties in South Carolina (Figure 1). All sites were in the Carolina Piedmont region and are a part of the greater Charlotte Metropolitan Area (City of Rock Hill n.d.). Rural and urban sites were distinguished using the 2010 South Carolina Census data in the same manner as Santana and Armstrong in Alabama (2017). Rural sites were defined as any location with 15-999 residents per square kilometer. Urban sites were considered and defined as any location with 1,000-13,800 residents per square kilometer.

The seven surveyed rural sites included four state parks: Andrew Jackson in Lancaster County, Landsford Canal in Chester County, Chester in Chester County and Kings Mountain in York County (Table 1). An additional state-owned rural site surveyed was Draper Wildlife Management Area in York County (Table 1). I also surveyed two private properties within York County, which I refer to as the Chappell Farm and the Langley Property (Table 1). All rural sites included open areas with wide corridors and trails, which are landscape features that coyotes are known to use and the private properties had open areas that included fields frequently altered for agricultural use (corn and cotton; Atwood et al. 2004).

Urban sites included land that runs along public trails at Carolina Piedmont Medical Center Trail (Riverwalk) in Rock Hill, SC and Founders Trail in Fort Mill, SC which both run alongside the Catawba River (Table 1). Additionally, I sampled the Anne Springs Close Greenway in Fort Mill and, within Rock Hill, at Tech Park, the Rock Hill Regional Airport and the Winthrop University Research Complex on the Winthrop University Campus (Table 1). Sites were selected based on information from the Nation Ford Land Trust and through knowledge of Winthrop professors concerning local coyote populations.

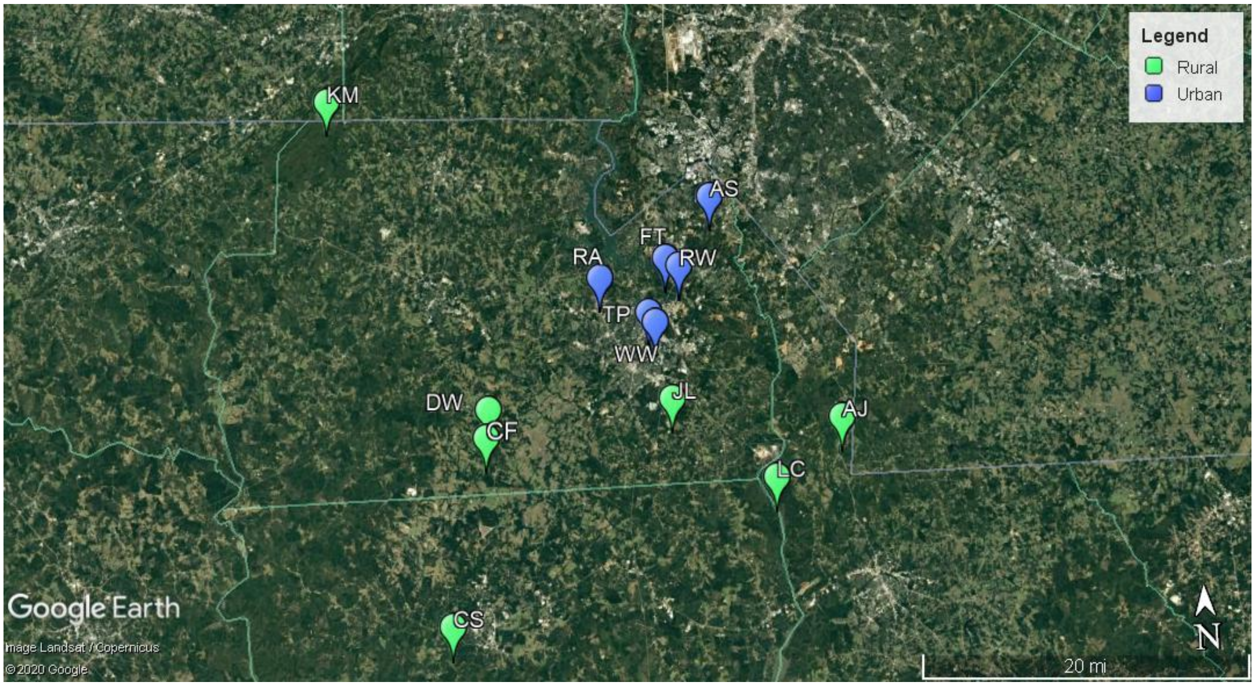

Figure 1: Map depicting study sites. KM: Kings Mountain State Park, DW: Draper Wildlife Management Area, CF: Chappell Farm, CS: Chester State Park, RA: Rock Hill-York County Airport, TP: Tech Park, WW: Winthrop Woods, FT: Founder's Trail, RW: Riverwalk, AS: Anne Springs Close Greenway, JL: Langley Property, LC: Landsford Canal State Park, and AJ: Andrew Jackson State Park.

Field Methods

Sites were visited and searched for scats every two weeks from February 2019 until the end of November 2019 to account for seasonal variation in diet. Seasons were categorized using Poessel et al. (2016) and covered three biological seasons: breeding (1 January-30 April), pup-rearing (1 May-31 August), and dispersal (1 September- 31 December). Trails and corridors were walked to search for possible scats. Surveyed trails were selected based on width and connection to open areas such as fields or corridors. These trails were walked for a duration of 45 minutes to 1.5 hours depending on trail length. Some of the named trails surveyed included the CCC trail and Farm trail at Kings Mountain State Park and the Blue Star trail and Haigler Loop at Anne Springs Close Greenway.

Table 1: Location data for thirteen research sites. Number of visits is rough estimate due to limitations from trail closures or flooding.

Location	Coordinates	Number of visits	Estimated distance traveled per visit (km)
Chappell Farm	34°50'26.17"N 81°11'29.14"W	~22	~1.50
Draper Wildlife Management Area	34°51'55.30"N 81°11'15.45"W	~22	~1.00
Rock Hill Airport	34°58'36.63"N 81° 3'31.46"W	~22	~0.75
Winthrop Woods	34°56'36.69"N 81° 0'28.86"W	~22	~1.00
Landsford Canal State Park	34°47'28.12"N 80°52'50.23"W	~22	~4.80
Andrew Jackson State Park	34°50'26.47"N 80°48'21.07"W	~22	~1.50
Anne Springs Close Greenway	35° 2'38.98"N 80°56'1.53"W	~22	~5.20
Founder's Trail	34°59'28.61"N 80°59'10.10"W	~22	~9.00
Chester State Park	34°40'35.60"N 81°14'15.18"W	~22	~2.10
Tech Park	34°56'4.39"N 81° 0'4.86"W	~22	~0.50
Langley Property	34°51'56.95"N 80°59'16.98"W	~22	~1.00
King's Mountain State Park	35° 8'57.43"N 81°20'50.19"W	~22	~12.80
River Walk	34°59'1.59"N 80°58'18.39"W	~22	~8.00

Field guides were used to distinguish between coyote scats and those of foxes and domestic dogs (Carr et al. n.d.). Only samples unambiguously identified as of coyote origin were collected. Scats collected at each site were placed in individual 0.946-liter Ziploc bags labeled with the date, location, and a unique collection number and returned to Winthrop University.

Camera traps (Bushnell HD Model 119476) were also used throughout the study period to try and identify individual coyotes. Due to limitations in number of camera traps, those deployed were at sites with the strongest evidence of coyote presence, the Chappell Farm and Winthrop Woods locations.

Macroscopic Analysis

Once collected, scats were placed in a -80°C freezer for at least 24 hours to kill any latent parasites (Morey et al. 2007). Scats were then thawed and placed in an oven to dry for at least a day before analysis; both frozen and dry masses of individual scats were recorded, but only dry masses were used for analysis. A subsample of around 1-2 mg for each scat was collected for stable isotope analysis after macroscopic materials were sorted from it.

Macroscopic components of the scats were analyzed by sorting samples using a 1mm mesh sieve. Visible items were sorted into eight categories: hair, bone, seeds, vegetation, insect exoskeletons, feathers, claw and hair and anthropogenic materials. The first seven categories were then identified to the lowest taxonomic level using appropriate dichotomous keys and identifications by with Winthrop professors (Stains 1958). For a given sample, the dry mass of each macroscopic category was recorded and used to estimate its percent contribution to a scat.

Stable Isotope Analysis

Once macroscopic components were sorted, the matrix that passed through the sieve was used for stable isotope analysis in a manner similar to Reid and Koch (2017). However, unlike Reid and Koch (2017) who rinsed the matrix, I ground the samples to a fine powder. Samples were dried in an oven and then I weighed 1-2 mg subsamples into encapsulation tins. Samples were sent to the Stable Isotope Laboratory at University of Georgia for analysis of their carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values.

Statistical Analysis

When possible, data were analyzed using IBM SPSS Statistics v.25, although some computations were done by hand. To assess the relative occurrence of macroscopic components between rural and urban habitats, a Scheirer-Ray-Hare non-parametric two-way ANOVA was used with the factors being habitat type and component type (Dytham 2011). The factor component type was measured using dry weight of components. Relative occurrence was considered percent occurrence (PO) using PO_i (%) = (n_i / $\sum n_i$) *100, where each prey item *i* is expressed as a percentage of the total number of occurrences of all food items (Larson et al. 2015). For statistics relating to macroscopic components, the categories of hair, bones, hair and claws, and feathers were combined into one category referred to as “vertebrates”. The presence of vertebrate taxonomic groups present in scats between rural and urban habitats and across seasons was analyzed using a Chi-squared test (Heath 1995). Season 3 (dispersal) was excluded from the Chi-squared test as its sample size (one) was too small. A Student's t-test was used to assess the difference between rural and urban habitats in $\delta^{13}C$ and $\delta^{15}N$ isotope values. To analyze the relationship across seasons of $\delta^{13}C$ and $\delta^{15}N$ levels between rural and urban habitats, a Scheirer-Ray-Hare test was used. Data not normally distributed were transformed using $\log_{10}$ transformations. All tests employed an alpha level of 0.05.

Results

A total of 20 scats were found from four of the surveyed locations (Table 2). Ten scats were collected from rural sites and ten were collected at urban sites. Of the ten collected at rural sites, three were found during the breeding season, six were found during pup-rearing season, and one was found during dispersal (Table 2). Of the ten scats collected at urban sites, four were collected during the breeding season, three during pup-rearing, and three during the dispersal season (Table 2). Only two individual coyotes were identified using camera traps (Figures 2 and 3).

Figure 2: Coyote captured by camera trap at rural site, Chappell Farm, York County, South Carolina.

Figure 3: Coyote captured by camera trap at urban site, Winthrop Woods, York County, South Carolina.

Table 2: Total number of scats found in all thirteen locations throughout this study period. Scats are sorted by season of collection: breeding (1 January-30 April), pup-rearing (1 May-31 August), and dispersal (1 September- 31 December).

Location	Total # of scats collected	Breeding	Pup-rearing	Dispersal
Chappell Farm	4	3	0	1
Draper Wildlife Management Area	0	0	0	0
Rock Hill Airport	0	0	0	0
Winthrop Woods	9	4	2	3
Landsford Canal State Park	0	0	0	0
Andrew Jackson State Park	0	0	0	0
Anne Springs Close Greenway	0	0	0	0
Founder's Trail	0	0	0	0
Chester State Park	0	0	0	0
Tech Park	1	0	1	0
Langley Property	6	0	6	0
King's Mountain State Park	0	0	0	0
River Walk	0	0	0	0

Macroscopic Analysis

I found no significant differences in occurrence of coyote scat macroscopic components between rural and urban habitats in my study area in the Piedmont region of South Carolina (Scheirer-Ray-Hare Test; X^2=2.79, df=1, p=0.100). However, there was a significant difference in the relative weight of macroscopic component categories consumed overall but not between rural and urban habitats (Scheirer-Ray-Hare Test; X^2=36.59, df=4, p≤0.001).

The predominant macroscopic components within scats from both rural and urban habitats were hair, bones and vegetation. In rural habitats, the distribution was: hair (22.58%), bones (32.26%), vegetation (22.58%) (Figure 4). In urban scats the distribution was hair (22.58%), bones (22.58%), and vegetation (25.81%) (Figure 4). Component category demonstrated a significant difference in distribution of hair, bone, and vegetation within both rural and urban habitats (Scheirer-Ray-Hare Test; X^2=10.146, df=2, p=0.01). However, habitat type had no effect on the distribution of hair, bone and vegetation (Scheirer-Ray-Hare Test; X^2: 0.565 df=1, p=0.45). Nor was there an interaction between habitat type and component category (Scheirer-Ray-Hare Test; X^2= 1.764, df=2, p=0.41).

There was no significant difference between vertebrate taxonomic groups present when comparing rural and urban habitats (Chi-squared Test: X^2=0.175, df=2, p=0.916). Season had no effect on taxonomic group occurrence in either rural or urban habitats (Chi-squared Test: season 1: X^2= 0.0748, df=2, p=0.9633; season 2: X^2= 0.8929, df=2, p=0.6399).

Hair identification from scats indicated the presence of members of three mammalian orders: Carnivora (55%), Rodentia (35%), and Lagomorpha (70%) (Supplemental Table 1, S1). Carnivora hair samples identified to species with certainty were from coyote (*Canis latrans),* grey fox (*Urocyon cinereoargenteus*), striped skunk (*Mephitis mephitis*) and domestic cat (*Felis catus*) (Figure 5). The presence of coyote hair was assumed to be from allogrooming and/or autogrooming. Species of Rodentia identified from hair were hispid cotton rat (*Sigmodon hispidus*) and eastern grey squirrel (*Sciurus carolinensis*) (Figure 5). The Eastern cottontail (*Sylvilagus floridanus*) was the only representative of Lagomorpha (Figure 5). Some scats had more than one mammalian order present: 20% had all three orders present, 40% had two, 20% had one, and 20% had no hairs present. Prey hairs are assumed to be present as a result of hunting or scavenging by coyotes. Feathers were identified as belonging to domestic chickens (*Gallus gallus*). Insect exoskeletons identified belonged to orders Orthoptera (grasshoppers) and Coleoptera (beetles). Vegetation consisted mostly of grasses (Poaceae). Identifiable seeds were from persimmons (*Diospyros virginiana*) and grasses.

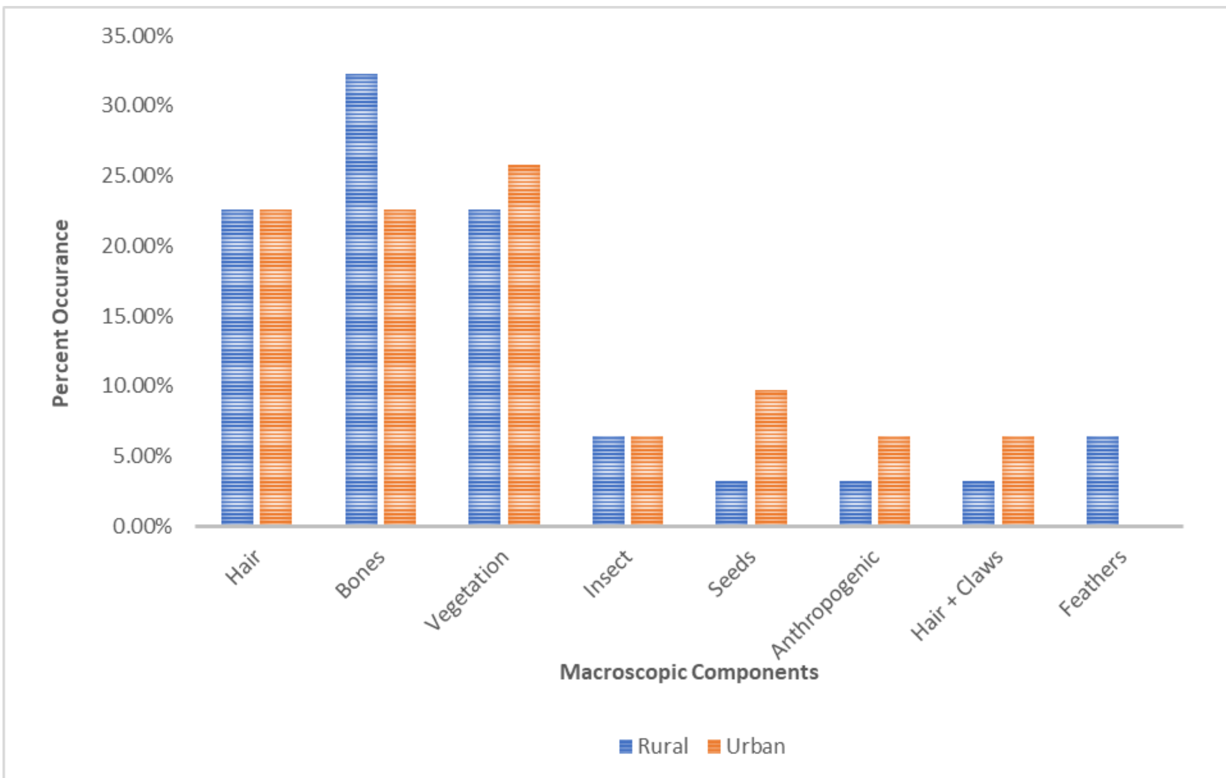

Figure 4: Percent occurrence of macroscopic components in rural and urban coyote scats.

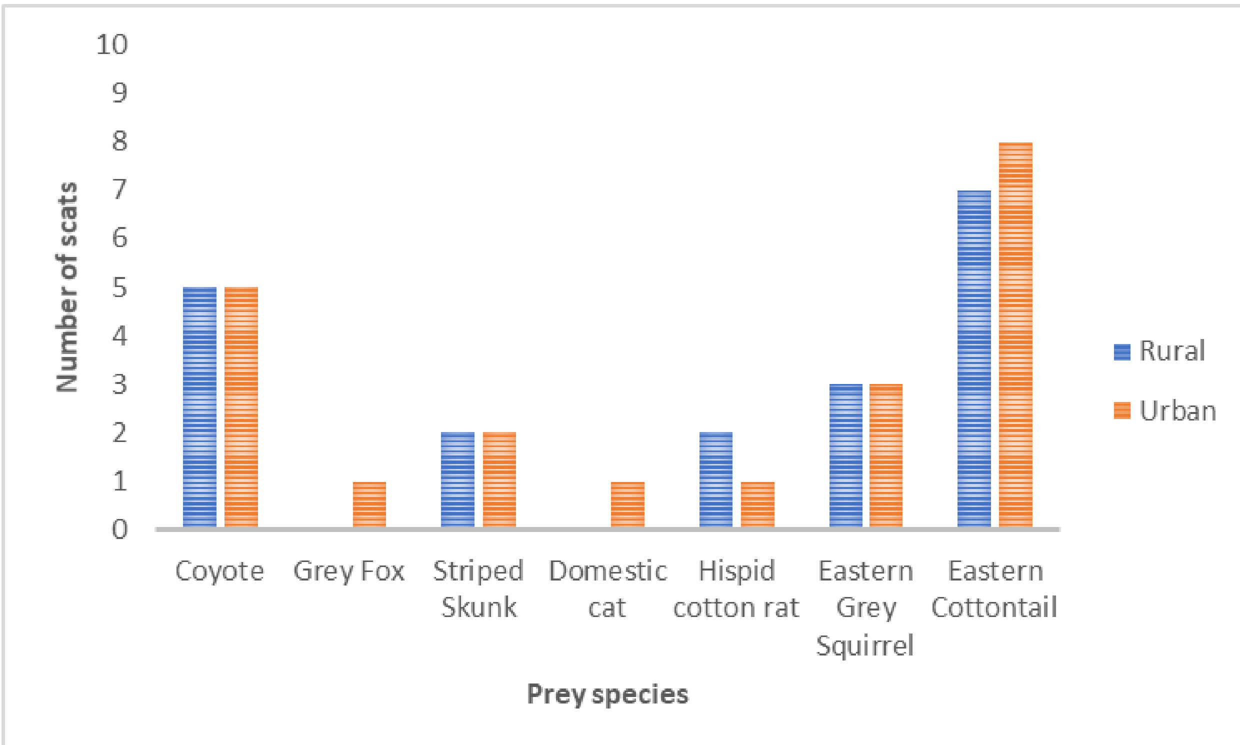

Figure 5: Prey species presence in macroscopic analysis in rural and urban scats.

Stable Isotope Analysis

There was no significant difference in $\delta^{13}C$ values in coyote scats between rural and urban environments overall (Student's t-test: t=-0.93, df=18, p= 0.927). Neither was there a significant difference in $\delta^{15}N$ values in coyote scats between rural and urban environments overall (Student's t-test: t=1.516, df= 18, p=0.147). Season had no effect on the distribution of $\delta^{13}C$ values in coyote scats (Scheirer-Ray-Hare: X^2=0.613, df=2, p=0.74). Habitat type also had no effect on the seasonal distribution of $\delta^{13}C$ values in coyote scats (Scheirer-Ray-Hare: X^2=1.496, df=1, p=0.22). There was no interaction between seasons and habitat type regarding $\delta^{13}C$ values (Scheirer-Ray-Hare: X^2=3.439, df=2, p=0.18) Similarly, seasons had no effect on the distribution of $\delta^{15}N$ values in coyote scats (Scheirer-Ray-Hare: X^2=2.758, df=2, p=0.25). Habitat type had no effect on distribution of $\delta^{15}N$ values in coyote scats (Scheirer-Ray-Hare: X^2=0.091, df=1, p=0.76). There was no interaction between seasons and habitat type regarding $\delta^{15}N$ values (Scheirer-Ray-Hare: X^2=01.204, df=2, p=0.55).

Discussion

Coyotes have become one of the top predators in urban ecosystems and are considered "urban adapters". Their success is attributed to a great degree of flexibility in their diet and their incorporation of novel food resources available in urban ecosystems. Previous research has investigated the potential differences in diet composition between rural and urban coyotes, as mentioned earlier (Fedriani et al 2001; Santana and Armstrong 2017; McClure et al. 1995; Poessel et al 2017a; Grigione et al. 2011; Morey et al. 2007). While those studies were focused primarily in the western and northern United States, in South Carolina, Schrecengost et al. (2008) reported the only known information about the diet of rural coyotes in the state. However, there has not been any research comparing the diets of rural and urban coyotes in South Carolina, including the Piedmont region.

Macroscopic and stable isotope analysis of coyote scats was utilized in the present study to assess the effect of available anthropogenic food sources on coyote diet in this region. Stable isotope analysis has only recently been used to study the effects of anthropogenic food sources on diet of organisms from scats (Newsome et al. 2010). My overall hypothesis proposed that coyotes inhabiting urban areas were exploiting dietary resources that are unintentionally and, in rare cases, intentionally made available through the presence of humans (Baker 2007). Thus, I hypothesized that overall anthropogenic foods would be higher in coyote scats collected from urban sites than from their rural counterparts. However, this was not entirely the case with coyote diets in the Piedmont region of South Carolina.

Macroscopic Analysis

Habitat Effects

There was no difference in the dry masses of macroscopic components of coyote scats between rural and urban habitats. That finding supports the idea that coyotes are making use of similar resources in both habitats, including small amounts of anthropogenic materials. Rural sites within the present study had illegally disposed refuse along roadsides and residential trash cans that could have contributed to anthropogenic materials in rural coyote food sources. Although occurring in low numbers in the present study, anthropogenic materials such as plastic and twine were found in two urban scats and one rural scat. These results are consistent with those of Santana and Armstrong (2017) who found no difference in anthropogenic materials in scats across an urban to rural gradient; they suggested the lack of difference was due to the consistent availability of human food across that gradient. Similarly, Grigione et al. (2011) found no significant difference in anthropogenic content between rural and urban habitats in Florida but noted that there was over twice as much anthropogenic material in scats from urban sites as those from rural areas. Morey et al. (2007) also reported a low occurrence of anthropogenic food items (2-25%) in coyote scats in Chicago, although they also reported personal observations of coyotes eating roadside trash and materials from dumpsters.

While there was no statistical difference in anthropogenic materials between habitats in this study, one of the urban scats was almost entirely composed of human refuse, primarily plastic and some cloth; one component of the scat was an almost complete wrapper from a package of dog food. However, anthropogenic food sources were also present in rural scats, with plastic pieces found in one scat and domestic chicken feathers in another. Landowners near the site where the scat with chicken feathers was collected in it reported chickens missing from their farm.

One private property surveyed in this study was near an elementary school, which could have resulted in increased levels of anthropogenic content from students littering. One of the scats containing anthropogenic materials was collected at this site. Similarly, Lukasik and Alexander (2008) in Canada reported that in one study site, higher trash presence was probably due to a nearby elementary school.

Within each habitat type there were differences between the categories of macroscopic components, suggesting that coyotes are utilizing some resources over others. Vertebrate components (hair and bone) were predominant in scats in both habitats. Bone was most prevalent in rural habitats (32.26%) while vegetation (25.81%) was most prevalent in urban habitats compared to other components. Vegetation may have been more prevalent due to the planting of ornamental species of plants and a nearby greenhouse at one urban site. This was in contrast to Grigione et al. (2011) who found vegetative matter to occur in highest abundance in rural scats. Seeds, particularly from grass and persimmons were also more prevalent in urban scats than in rural in this study. In South Carolina, the only other known coyote diet study (Schrecengost et al. 2008) also found persimmons to be prevalent in late fall/early winter, the plant’s normal fruiting time; that was consistent with what this study found.

There was no difference regarding vertebrate taxonomic groups present when comparing scats from rural and urban habitats. As coyotes in this study were consuming similar prey in both habitats, those taxa (Carnivora, Rodentia, and Lagomorpha) are likely consistently available in both habitats. Both Poessel et al. (2017a) and Fedriani et al. (2001) report that rodents were the dominant prey category across varying levels of urbanization.

Foxes and domestic cats, identified from hair, were only present in urban coyote scats. The presence of domestic cat hairs in urban areas could have come from both pet and feral cats. Coyotes reduce feral cat populations which is consistent with the mesopredator release hypothesis (Crooks and Soule 1999). The mesopredator release hypothesis states that the decline of the most common large predator would result in the ecological release of native and exotic mesopredators, and that increased predation by these mesopredators would result in higher mortality and local extinction rates of prey groups such as small mammals and birds (Crooks and Soule 1999). It is well established that cats, both feral and domestic, are the equivalent of an ecosystem disaster, killing an estimated 1.3 to 4.0 billion birds and 6.3 to 22.3 million mammals each year in the United States (Loss et al. 2013). If the mesopredator release hypothesis is correct, coyotes should reduce predation by feral and pet cats and therefore allow populations of native of birds and mammals to increase. Domestic cat hair found in urban scats suggests that coyotes are either opportunistically hunting cats or perhaps scavenging on roadkill animals.

Seasonal Effects

I hypothesized that during dispersal season (1 September- 31 December) there would be higher levels of anthropogenic foods in urban scats compared to other seasons as natural foods become scarcer over that span. However, there was no difference in levels of anthropogenic food sources between rural and urban habitats across seasons. Thus, anthropogenic food sources appear to have been equally available throughout the year in both habitats. Furthermore, the distribution of taxonomic groups found in scats was similar across two seasons (breeding and pup-rearing) between rural and urban coyote scats analyzed (the third, dispersal, was excluded because of its small sample size). A study in South Carolina looked at the seasonal variation in the diet of rural coyotes (Schrecengost et al. 2008). They investigated seasonal variability in coyote diet and found that plant matter dominated from May to November in 2005 and again from June to July in 2006 while animal food items dominated from December to April, roughly equivalent to breeding in this study (Schrecengost et al. 2008). Furthermore, they found that animal foods (white-tailed deer, wild hogs, rabbits and grasshoppers) dominated rural coyote diet from December through April. Poessel et al. (2017a) found that in Denver there was a difference in the seasonality in coyote diet, likely due to the dramatic changes in seasons there. Mammals were more common in scats in December, March, April, and June in both high- and low-density sites (Poessel et al. 2017a).

Stable Isotope Analysis

Habitat effects

My hypothesis that $\delta^{13}C$ values would be higher in scats collected from urban sites than from their rural counterparts was not supported. Higher $\delta^{13}C$ isotope values indicate potential anthropogenic food sources because processed foods and livestock feed contain high levels of corn which is more enriched in ^{13}C than in other plant food sources (Jahren and Kraft 2008). Stable isotope analysis showed no difference in $\delta^{13}C$ isotope values between urban and rural coyote scats across the various study sites. This contrasts with Newsome et al. (2010), who found higher values of $\delta^{13}C$ in kit fox diet due to anthropogenic food sources in the Central Valley of California. The lack of difference in carbon isotope values in the present study could mean that coyotes have roughly equal access to anthropogenic food sources in both urban and rural areas. These food sources could include human food waste and pet food, particularly dog food. Moreover, because corn was present in rural sites, if coyotes also made use of this crop then the carbon isotopes values in their scats would be high.

I also found no difference in $\delta^{15}N$ isotopes between rural and urban habitats. This further contrasts with Newsome et al. (2010), who found low values of $\delta^{15}N$ in kit fox diets in urban areas. Nitrogen isotopes are often used as indicators of protein levels in food webs, as species belonging to higher trophic levels contain increased levels of $\delta^{15}N$ (DeNiro and Epstein 1981).

Seasonal Effects

I hypothesized that during dispersal season $\delta^{13}C$ values would be higher as coyotes make use of anthropogenic food sources because natural food sources become scarcer. Values of $\delta^{13}C$ isotope did not differ across seasons, again suggesting that the use of anthropogenic materials is consistent across habitats and seasons. Similar to $\delta^{13}C$ values, $\delta^{15}N$ values did not differ between rural and urban habitats nor across seasons.

To assess the relationship between $\delta^{13}C$ and $\delta^{15}N$, I utilized a mathematical model called an isotopic mixing model (EPA 2017). Isotopic mixing models are used to determine the proportion of various sources in a material and are used in dietary studies to assess where an organism falls on a food web

(EPA 2017). A strictly carnivorous organism typically would show high $\delta^{15}N$ and low $\delta^{13}C$ due to their high protein consumption (Figure 6). In contrast, herbivores typically show low $\delta^{15}N$ and higher $\delta^{13}C$ due to their consumption of carbon-fixing plants. Humans, who are generally considered omnivores, would have high $\delta^{15}N$ and high $\delta^{13}C$. Modern western humans are unique for omnivores in the fact that our diet is unexpectedly high in carbon due to our corn-based diet. In figure 6, there clearly is an overlap in rural and urban isotope distributions showing no statistical difference between habitats. This supports the idea that coyotes are generalist omnivores as their diet falls between pure carnivores, pure herbivores, and modern western humans.

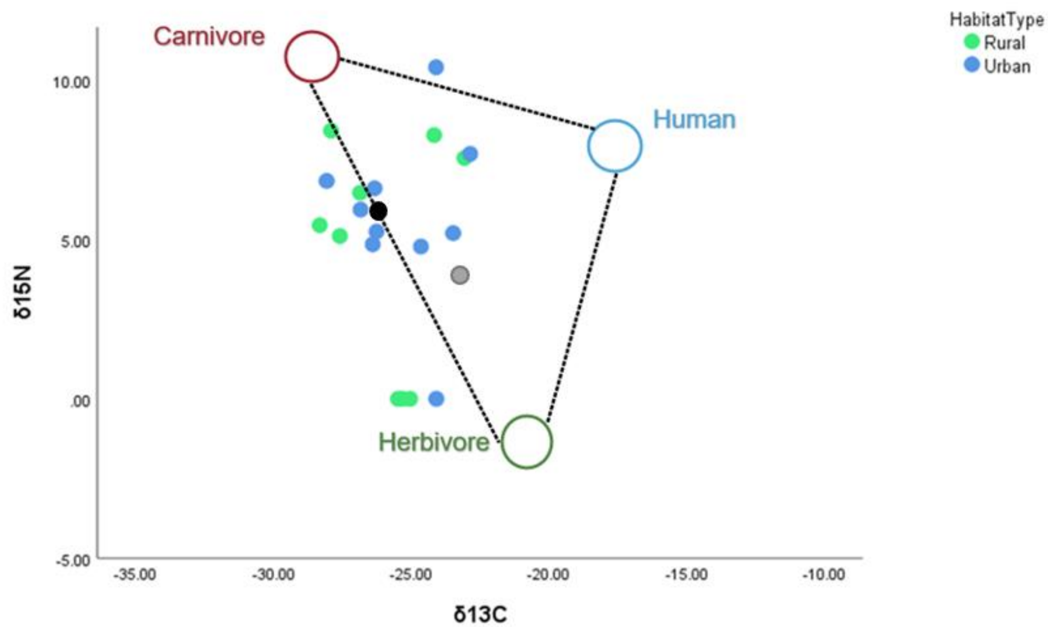

Figure 6: Isotopic mixing model (Hopkins and Ferguson 2012) of rural and urban coyote scats. Black circle represents the average for urban scats. Grey circle represents the average for rural scats

Figure 6 represents the distribution of $\delta^{13}C$ and $\delta^{15}N$ in scats in rural and urban habitats modeled after Hopkins and Ferguson (2012). I found similar distributions of $\delta^{15}N$ isotopes in coyote scats as Hopkins and Ferguson (2012) did for another omnivorous mammal, the black bear (*Ursus americanus*). [One outlier point ($\delta^{13}C$-0.0, $\delta^{15}N$-0.0) was excluded on the rural graph as it didn't fit the scale of Hopkins and Ferguson (2012).] This further supports the idea that coyotes are generalist omnivores.

My hypotheses were not supported, as there was no difference either in macroscopic materials or $\delta^{13}C$ and $\delta^{15}N$ levels between rural and urban coyote scats. This does not indicate that coyotes are not consuming anthropogenic materials, but perhaps are exploiting anthropogenic foods equally across habitat types. There was no difference in dietary composition between rural and urban habitats, but anthropogenic food was found in two urban scats and one rural scat. The presence of illegally disposed garbage and residential trash cans could have allowed anthropogenic food sources to be as available in rural habitats as it is in urban and corn-based products across landscapes, which can bias $\delta^{13}C$ ratios.

Future Directions

This study is the first to assess the diet of rural and urban coyotes in the Piedmont region of the Carolinas. Within the last 40 years since coyotes expanded into the Carolinas there has been a dramatic change in the landscape due to urbanization. With increasing rates of development in the region, such as the 234-acre Carolina Panthers training facility in Rock Hill, SC (Hughes 2019), the opportunity for coyotes to exploit anthropogenic resources will increase and in turn likely raise occurrences of conflict. This present study sets a foundation for further research on coyote diets in the region. Future dietary studies should utilize stable isotope analysis, which has become the new cost-effective standard for dietary analysis as it can identify digestible components of diet that can't be found through the traditional method of macroscopic analysis (Newsome et al. 2010; Reid and Koch 2017). Earlier studies noted that purely macroscopic analysis of scats in their studies did not account for consumption of anthropogenic foods such as dog food (Poessel et al. 2017a). However, Reid and Koch (2017) reported that compared to using components such as bone, hair, and muscle tissue, scat contained the lowest level of carbon isotopes. They also reported that when studying seasonal variation in diet, scat is the best compared to bone, hair, and muscle tissue because it shows a snapshot of a recent diet event.

A potential source of bias in this study can be attributed to having only a single investigator undertaking all the data collection and analysis. In contrast, Poessel et al. (2017a) utilized seventeen technicians and volunteers for scat collection and lab work. Further investigations should recruit assistants as well as conduct the study over a longer time. Previous studies have typically collected data over a two-year period (Santana and Armstrong 2017; Poessel et al. 2017a; Morey et al. 2007). Even longer collection periods should be standard, especially when assessing seasonal variation in diet. Furthermore, true independence of samples was not possible in this study as scats collected from the same site may have originated from the same individuals. Though camera traps were used to attempt to identify individuals, only two were captured from two different sites.

Coyote presence in urban environments is often a controversial topic, especially when it come to the public's perception of them. Some people refer to coyotes as "invasive" claiming they don't belong in cities and comparing their presence to criminal behavior (Alexander and Quinn 2012). Close proximity has allowed some coyotes to habituate to humans and this often results in increased levels of conflict. Such conflict has resulted in aggressive management techniques such as trapping and killing coyotes (Urban Coyote Project n.d.). That practice involves killing multiple coyotes in an area to make sure the one nuisance coyote is removed. In western South Carolina, Schrecengost et al. (2009) studied survival in rural coyotes and found that 60% of coyote mortality in the area can be attributed to hunting and trapping.

Such persecution by humans apparently influences the movement of coyotes. While lethal removal or simply relocation are two common methods for coyote management, both have been shown to be ineffective (Urban Coyote Project n.d.). Gese (2005) found that after the removal of nuisance coyotes in an area there was an initial reduction in pack size and a decrease in density. However, after eight months, coyotes returned to the same population levels as those prior to the removal (Gese 2005). Organizations such as the Urban Coyote Project in Chicago work at discouraging these removal practices and often give advice on using negative stimuli such as loud noises and spraying with hoses to deal with nuisance coyotes to encourage the public to reduce habituation of coyotes to humans. Understanding how coyotes behave in urban areas, especially relating to their diet, can help prevent further conflict and inform management practices.

Appendix

(S1) Supplemental Table 1: Presence of mammal taxonomic groups identified from hair in scats of rural and urban coyotes. Boxes with a 1 indicates presence and 0 indicates lack of presence.

	Carnivora	Rodentia	Lagomorpha
WW#1	1	0	1
JL#5	1	1	1
CF#2	1	1	1
JL#3	0	0	1
JL#2	0	0	0
JL#4	0	0	0
JL#1	1	0	1
WW#9	1	0	1
WW#5	1	0	1
WW#3	0	0	1
CF#1	1	0	1
WW#7	1	1	1
WW#2	0	0	0
WW#4	0	1	0
WW#6	1	0	1
CF#4	0	1	0
CF#3	1	0	1
JL#6	0	0	0
TP#1	1	1	1
WW#8	0	1	1

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